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Temporal dynamics of motor cortex excitability during perception of natural emotional scenes

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Although it is widely assumed that emotions prime the body for action, the effects of visual perception of natural emotional scenes on the temporal dynamics of the human motor system have scarcely been investigated. Here, we used single-pulse transcranial magnetic stimulation (TMS) to assess motor excitability during observation and categorization of positive, neutral and negative pictures from the International Affective Picture System database. Motor-evoked potentials (MEPs) from TMS of the left motor cortex were recorded from hand muscles, at 150 and 300 ms after picture onset. In the early temporal condition we found an increase in hand motor excitability that was specific for the perception of negative pictures. This early negative bias was predicted by interindividual differences in the disposition to experience aversive feelings (personal distress) in interpersonal emotional contexts. In the later temporal condition, we found that MEPs were similarly increased for both positive and negative pictures, suggesting an increased reactivity to emotionally arousing scenes. By highlighting the temporal course of motor excitability during perception of emotional pictures, our study provides direct neurophysiological support for the evolutionary notions that emotion perception is closely linked to action systems and that emotionally negative events require motor reactions to be more urgently mobilized.

Keywords: emotional scenes; motor reactions; neural dynamics; corticospinal excitability; transcranial magnetic stimulation; personal distress

INTRODUCTION

Perceiving and immediately reacting to potential threats are critical for survival (Darwin, 1872). Negative stimuli require perceptual processing and action resources to be more intensely and urgently mobilized to minimize negative consequences associated with unpleasant cues. In support of this view, behavioral and electrophysiological studies have found that unpleasant stimuli are detected more quickly (Hansen and Hansen, 1988; Fox *et al.*, 2000; Öhman *et al.*, 2001) and are associated with larger early (100–200 ms) occipito-temporal components of event-related potentials (ERPs) relative to pleasant or neutral stimuli (Schupp *et al.*, 2003; Smith *et al.*, 2003; Pourtois *et al.*, 2004; for a review, see Olofsson *et al.*, 2008) suggesting a rapid bias in visual attention allocation with greater resources devoted to negative stimuli (Vuilleumier, 2002; Carretié *et al.*, 2009). This 'negative' bias may reflect interactions between cortical and subcortical structures, as suggested for example by the rapid amygdala activation during processing of aversive stimuli (Oya *et al.*, 2002; Tamietto and De Gelder, 2010) and the reduced amplitudes of occipito-temporal ERP components for negative stimuli when the amygdala is lesioned (Rotshtein *et al.*, 2010).

The impact of negative bias has also been explored at the motor level. For example, studies indicate that while both positive and negative stimuli can modulate motor behavior (e.g. by favoring approach and avoidance movements, respectively), negative stimuli are particularly adept at evoking rapid reactions in the observer (Cacioppo, 1993; Bradley *et al.*, 2001; Freina *et al.*, 2009; Coombes *et al.*, 2005, 2009; Naugle *et al.*, 2010) providing support for the evolutionary contention that increased motor readiness in the face of threat may best secure survival of the organism (Lang *et al.*, 2000; Öhman and Mineka, 2001; Carretié *et al.*, 2009; Frijda *et al.*, 2009). These findings would also suggest that seeing emotionally negative stimuli while at rest should automatically trigger short-latency activation of the motor representation of the dominant hand.

Single-pulse transcranial magnetic stimulation (TMS) is a valuable way to noninvasively stimulate the human motor cortex in resting conditions and thus instantaneously assess changes in the excitability of distinct corticospinal representations of the body (Hallet, 2007; Serino *et al.*, 2009; Avenanti *et al.*, 2012b). This approach has been classically used to probe motor excitability when imagining (Fadiga *et al.*, 1999; Fourkas *et al.*, 2006), observing (Fadiga *et al.*, 2005; Urgesi *et al.*, 2010; Avenanti *et al.*, 2013a,b), planning or performing an action (Hoshiyama *et al.*, 1997; Hasbroucq *et al.*, 1999; Michelet *et al.*, 2010). The high temporal resolution of the technique and the possibility to distinguish between excitatory and inhibitory activity allows effective exploration of action-related dynamics and can provide direct information about how neural processing in the motor cortex unfolds over time (Prabhu *et al.*, 2007; Michelet *et al.*, 2010; Barchiesi and Cattaneo, 2013; Avenanti *et al.*, 2012a).

Recently, studies have used TMS to investigate the excitability of the hand representation in the left motor cortex during observation of natural emotional scenes. These studies have typically reported comparable increases in motor excitability for both emotionally positive and negative stimuli (Hajcak *et al.*, 2007; Baumgartner *et al.*, 2007; Coombes *et al.*, 2009; Borgomaneri *et al.*, 2012). Notably, however, in such studies, motor excitability was tested in a relatively late time window, i.e. at >300 ms after stimulus onset, when the amplitude of brain responses to emotional images is typically similar for positive and negative stimuli and likely reflects increased resource allocation to motivationally relevant cues as suggested by ERP studies (Cuthbert *et al.*, 2000; Keil *et al.*, 2002; Codispoti *et al.*, 2007; see also Olofsson *et al.*, 2008).

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Here we tested the hypothesis that a greater increase in excitability of the left motor cortex occurs for negative stimuli before increased motor reactivity for positive stimuli can be detected. We capitalized on ERP studies showing that responses in the visual system are: (i) larger for negative stimuli in an early temporal window (~100–200 ms) and (ii) similar for positive and negative stimuli at a later time (~300–600 ms) (Vuilleumier, 2002; Olofsson *et al.*, 2008). We reasoned that, to ensure survival, action reactivity should be closely coupled with visual processing and thus we predicted greater facilitation of the hand motor representation for negative stimuli in an early time window (at 150 ms from stimulus onset) followed by a comparable motor facilitation for both negative and positive stimuli (at 300 ms as in Borgomaneri *et al.*, 2012). To test these hypotheses we administered single-pulse TMS over the hand region of the left motor cortex to induce motor-evoked potentials (MEPs) in right hand muscles while participants observed and actively categorized positive, neutral and emotionally negative visual scenes from the International Affective Picture System (IAPS) database. Emotional pictures in the IAPS typically depict humans in emotionally arousing scenarios (e.g. smiling or distressed individuals, or people in sexual or threatening contexts, etc.) that may also induce empathy-related processing or personal distress (Lang *et al.*, 1999, 2000; Lamm *et al.*, 2007, 2008; Morelli *et al.*, 2012); notably, studies have shown that stable empathy or personal distress dispositions predict motor reactivity during social perception (Gazzola *et al.*, 2006; Avenanti *et al.*, 2009a; Minio-Paluello *et al.*, 2009; Avenanti *et al.*, 2010; Lepage *et al.*, 2010; Ferri *et al.*, 2010). Thus we investigated whether empathy and personal distress dispositions predicted the magnitude of motor reactivity to the different classes of pictures.

MATERIALS AND METHODS

Participants

Fourteen healthy participants (six men, mean age ± SD: 24.1 ± 1.4 years) took part in the study. All the subjects were right-handed according to a standard handedness inventory (Briggs and Nebes, 1975), had normal or corrected-to-normal visual acuity in both eyes, and were naïve as to the purposes of the experiment. None of the participants had neurological, psychiatric or other medical problems or any contraindication to TMS (Rossi *et al.*, 2009). Participants provided written informed consent, and the procedures were approved by the ethics committee at the Psychology Department of Bologna University and were in accordance with the ethical standards of the 1964 Declaration of Helsinki. No discomfort or adverse effects during TMS were reported or noticed.

Visual stimuli

Color pictures from the IAPS database (Lang *et al.*, 1999; Figure 1A) were presented on a 19-inch screen located 80 cm away from the participants. A total of 32 pleasant, 32 unpleasant and 32 neutral pictures (subtending a 21.2° by 16.2° region) were shown. The stimuli were already included in previous TMS studies (Hajcak *et al.*, 2007; Van Loon *et al.*, 2010; Borgomaneri *et al.*, 2012) and are listed in Supplementary Table 1.

Transcranial magnetic stimulation and electromyography recording

MEPs induced by TMS were recorded from the right first dorsal interosseus (FDI) and abductor pollicis brevis (APB) with a Biopac MP-35 (Biopac, USA) electromyograph. We selected these two muscles to compare our results with previous studies that explored the excitability of the FDI (Oliveri *et al.*, 2003), the APB (Hajcak *et al.*, 2007; Van Loon *et al.*, 2010) or both the FDI and APB motor representations

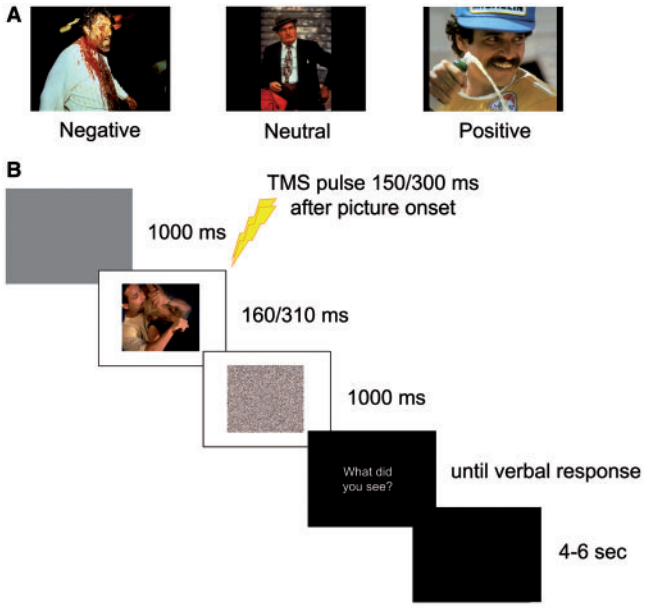

Fig. 1 Examples of visual stimuli and trial sequence.

(Borgomaneri *et al.*, 2012) during the observation of emotional pictures. Electromyographic (EMG) signals were band-pass filtered (30–500 Hz), sampled at 5 kHz, digitized and stored on a computer for offline analysis. Pairs of silver-chloride surface electrodes were placed in a belly-tendon montage with ground electrodes on the wrist. A figure-of-eight coil connected to a Magstim Rapid2 stimulator (Magstim, Whitland, Dyfed, UK) was placed over the left M1. The intersection of the coil was placed tangentially to the scalp with the handle pointing backward and laterally at a 45° angle away from the midline. Using a slightly suprathreshold stimulus intensity, the coil was moved to determine the optimal position from which maximal amplitude MEPs were elicited in the contralateral FDI muscle. The optimal position was then marked on the scalp to ensure correct coil placement throughout the experiment. The intensity of magnetic pulses was set at 120% of the resting motor threshold (rMT), defined as the minimal intensity of stimulator output that produces MEPs with amplitudes of at least 50 μV in the higher threshold muscle with 50% probability (Rossini *et al.*, 1994). This way a stable signal could be recorded from both muscles (Avenanti *et al.*, 2007). The absence of voluntary contractions was continuously visually verified throughout the experiments. When muscle tension was detected the experiment was briefly interrupted and subjects were invited to relax.

Procedure

The experiment was programmed using Matlab software to control picture presentation and to trigger TMS. MEPs were collected in four blocks. The first and the last blocks (10 trials each) served as baseline: subjects kept their eyes closed with the instruction to imagine watching a sunset at the beach (Fourkas *et al.*, 2008; Tidoni *et al.*, 2013) while receiving TMS over M1 (interpulse interval ~10 s). In the other two blocks (48 trials each) subjects performed an emotion evaluation task, in which they were presented with a picture and were asked to categorize it as positive, negative or neutral. It is held that active categorization maximizes the chance of detecting emotion-specific modulations in different brain regions, including the motor system as suggested by previous imaging (Gur *et al.*, 2002; Hariri *et al.*, 2003; Habel *et al.*, 2007), TMS (Oliveri *et al.*, 2003) and ERP studies (Mikhailova and Bogomolova, 2000; Hajcak *et al.*, 2006). A gray screen (1000 ms duration) indicated the beginning of the trial. This

was followed by a test picture lasting 160 or 310 ms projected at the center of the screen (Figure 1B) and by a TMS pulse delivered at 150 or 300 ms after picture onset, respectively. The picture was followed by a random-dot mask (obtained by scrambling the corresponding sample stimulus by means of custom-made image segmentation software) lasting 1000 ms. Then the question 'What did you see?' appeared on the screen, and participants answered verbally (forced choice: positive, neutral or negative). An experimenter recorded the answer by pressing a computer key.

To avoid changes in excitability due to verbal response (Tokimura *et al.*, 1996; Meister *et al.*, 2003), participants were invited to answer only during the question screen, a few seconds after the TMS pulse (Tidoni *et al.*, 2013). After response, the screen appeared black for 4–6 s. This way the interpulse interval was >10 s, thereby avoiding changes in motor excitability due to TMS *per se* (Chen *et al.*, 1997). To reduce the initial transient-state increase in motor excitability, before each block two magnetic pulses were delivered over M1 (interpulse interval >10 s). Each baseline and experimental block lasted ~2 and 10 min, respectively. At the end of the TMS sessions, all stimuli (shown in a randomized order for 160 and 310 ms as in the TMS experiment) were presented to subjects, who were asked to rate arousal and valence of each picture using an electronic 5-point Likert scale. Arousal and valence ratings were collected in two separate blocks whose order was counterbalanced across subjects. Afterwards, to assess empathy and personal distress dispositions, subjects were asked to complete the Interpersonal Reactivity Index (IRI) (Davis, 1996), a 28-item self-report survey that consists of four subscales, namely Perspective Taking (PT, that assess the tendency to spontaneously imagine and assume the cognitive perspective of another person), Fantasy scale (FS, that assess the tendency to project oneself into the place of fictional characters in books and movies), Empathic Concern (EC, that assess the tendency to feel sympathy and compassion for others in need) and Personal Distress (PD, that assess the extent to which an individual feels distress in emotionally distressing interpersonal contexts). PT and FS assess cognitive components of empathy, while EC and PD correspond to the notions of other-oriented empathy reactions and self-oriented emotional distress, respectively (Davis, 1996). The PD subscale reflects an anxiety-related interpersonal reactivity that may interfere with mature forms of empathy; thus it tends to drop as the other scales rise and is negatively related to measures of overall social functioning.

Data analysis

Neurophysiological data were processed offline. Mean MEP amplitude values in each condition were measured peak-to-peak (in mV). Since background EMG is known to modulate the MEP amplitude, pre-TMS EMG was assessed by calculating the mean rectified signal across a 100 ms interval prior to TMS. MEPs with preceding background EMG deviating from the mean by >2 SD, were removed from further analysis (<5% and similarly distributed across conditions). It should be noted that pictures were presented for a relatively short time and online TMS may potentially distract participants. To assure that motor excitability reflected effective perception of IAPS stimuli, MEPs associated with incorrect picture classification were discarded from the analysis (see Supplementary Data for a discussion of the relation between classification accuracy and motor excitability). Mean accuracy in the emotion evaluation task was high (mean accuracy ± SD: 92 ± 4%). Accuracy and MEP data across subjects were normally distributed (as revealed by Shapiro–Wilk tests) and were analyzed by means of repeated measure analysis of variance (ANOVA). Significant effects in the ANOVAs were followed by *post hoc* analyses using Duncan tests corrected for multiple comparisons.

To investigate the relationships between early motor reactivity, dispositional empathy and personal distress, MEP contrasts (negative minus mean of positive and neutral pictures; mean of the two muscles) recorded at 150 ms and the four subscales of the IRI were entered into a correlation analysis. Partial correlations were computed between MEP contrasts and each IRI subscale while controlling for the remaining subscales. A further partial correlation analysis was computed on MEP contrasts (mean of positive and negative minus neutral pictures; mean of the two muscles) computed at 300 ms and the four IRI subscales. The two different MEP contrasts were chosen based on the results of the main ANOVA that showed a selective increase of motor excitability for negative pictures at 150 ms and a comparable increase of motor excitability for positive and negative pictures at 300 ms. MEP contrasts and IRI subscales were normally distributed as shown by Shapiro–Wilk tests. The significance level for the two correlation analyses was set at $P = 0.025$.

To confirm emotional features of the IAPS stimuli, we assessed mean scores of arousal and valence. These data were not normally distributed and thus were analyzed by means of nonparametric Friedman ANOVAs. Preliminary Wilcoxon test comparisons revealed that subjective ratings were statistically comparable for pictures presented for 150 and 300 ms (all $P > 0.27$) and thus data were collapsed across temporal conditions. Bonferroni-corrected planned Wilcoxon tests were used to analyze significant Friedman ANOVA effects.

RESULTS

Subjective judgements and classification accuracy of IAPS pictures

Subjective judgements confirmed emotional features of the IAPS stimuli (Table 1). Friedman ANOVAs carried out on mean valence and arousal scores were significant (all $\chi^2 > 26.14$ $P < 0.001$). Bonferroni-corrected planned Wilcoxon tests confirmed that valence was lower for negative relative to positive and neutral IAPS stimuli (all $P < 0.001$); moreover, positive IAPS stimuli obtained higher valence scores than neutral IAPS stimuli ($P < 0.001$). Arousal scores were higher for positive and negative IAPS stimuli relative to neutral IAPS stimuli (all $P < 0.001$).

Overall, classification accuracy during the TMS session was high. A Time (two levels: 150 ms and 300 ms) × Emotional scene (three levels: positive, neutral and negative) repeated measures ANOVA on percentage of correct responses indicated a main effect of Emotional scene ($F_{2,26} = 4.24$, $P < 0.05$). Duncan tests indicated greater accuracy for negative (mean accuracy ± SD; 97 ± 7%) relative to positive images (87 ± 14%, $P < 0.01$). Accuracy for neutral images (91 ± 11%) was statistically comparable to negative and positive images (all $P > 0.10$). There was no main effect of the factor Time, nor did it interact with Emotional scene (all $F < 1.98$, $P > 0.16$).

Temporal dynamics of motor excitability during perception of emotional scenes

Preliminary neurophysiological analyses assured that no change in excitability due to TMS *per se* was detected throughout the experiment

Table 1 Mean ± SD of arousal and valance ratings of stimuli in the different conditions

	Negative 150	Neutral 150	Positive 150	Negative 300	Neutral 300	Positive 300
Arousal	4.0 ± 0.8	1.3 ± 0.3	3.0 ± 0.6	4.0 ± 0.7	1.3 ± 0.2	3.0 ± 0.6
Valence	−1.4 ± 0.3	0.0 ± 0.05	1.1 ± 0.2	−1.3 ± 0.3	0.0 ± 0.1	1.1 ± 0.2

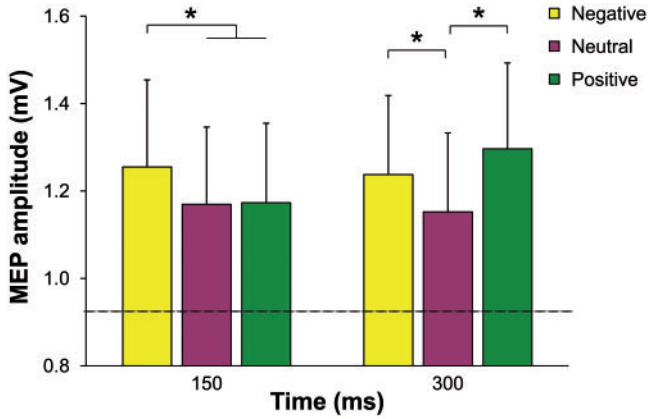

Fig. 2 MEP amplitude (in mV) recorded at 150 ms and 300 ms after presentation of negative, neutral and positive pictures (average of the two muscles, FDI and APB). The dashed line represents mean MEP amplitude during baseline blocks. Error bars indicate SEM. Asterisks (*) denote significant *post hoc* comparisons ($P < 0.05$).

and showed that motor excitability during the emotion evaluation task was greater relative to baseline levels (Figure 1; Supplementary Data).

To specifically investigate the effects of time and visual conditions on motor excitability, a Muscle (two levels: FDI and APB) × Time (two levels: 150 ms and 300 ms) × Emotional scene (three levels: negative, neutral and positive) repeated measures ANOVA on MEP amplitudes recorded during observation of IAPS stimuli was carried out. The analysis showed a main effect of Emotional scene ($F_{2,26} = 6.77$, $P < 0.01$) and, most importantly, a significant Time × Emotional scene interaction ($F_{2,26} = 4.76$, $P < 0.05$; Figure 2).

Post hoc analysis (performed with the Duncan test to account for multiple comparisons) indicates that at 150 ms MEP amplitude was greater during the observation of emotionally negative relative to both positive ($P < 0.05$) and neutral scenes ($P < 0.05$), which in turn did not differ from one another ($P = 0.93$). At 300 ms, MEP amplitude was greater during observation of both emotionally positive ($P < 0.01$) and negative ($P < 0.05$) relative to neutral scenes. No difference between positive and negative scenes was found ($P = 0.15$). No other main effects or interactions were significant, including those with the factor Muscle, indicating that similar changes in excitability were detected in the FDI and APB muscles (all $F < 3.04$, $P > 0.10$; Table 2).

Relation between personality and motor reactivity

The comparable motor facilitation for positive and negative IAPS images that we observed in the 300 ms condition confirms previous TMS studies that tested motor excitability within the same temporal frame (Borgomaneri *et al.*, 2012) or at a later time (Hajcak *et al.*, 2007; Baumgartner *et al.*, 2007; Coombes *et al.*, 2009). Notably, our study reveals that at an earlier stage of processing (150 ms) a selective increase of excitability for negative images occurs within the motor system. We explored whether interindividual differences in dispositional empathy and personal distress predicted the magnitude of these two neurophysiological effects.

An index of early motor reactivity for negative pictures (MEP contrast computed at 150) was entered into a partial correlation analysis with the four IRI subscales. Partial correlations showed that the PD was marginally significantly related to the MEP contrast at 150 ms ($r = 0.66$, $P = 0.027$; Table 3). This relationship strongly increased after the removal of one outlier with standard residuals $\leq 2\sigma$ ($r = 0.90$, $P < 0.001$; Figure 3).

An index of late motor reactivity for positive and negative pictures (MEP contrast computed at 300 ms) was entered into a further partial correlation analysis that showed no significant relationships with any of the IRI subscales (Table 3).

Table 2 Raw MEP amplitude ± SD (in mV) from the two target muscles during the experimental conditions

	Negative 150	Neutral 150	Positive 150	Negative 300	Neutral 300	Positive 300
FDI	1.50 ± 0.99	1.38 ± 0.81	1.38 ± 0.90	1.46 ± 0.89	1.37 ± 0.89	1.55 ± 0.95
APB	1.01 ± 0.50	0.96 ± 0.51	0.97 ± 0.47	1.01 ± 0.46	0.94 ± 0.46	1.04 ± 0.52

Table 3 Partial correlations between MEP contrasts and IRI subscales

IRI subscale	MEP contrast 150 ms		MEP contrast 300 ms	
	Correlation coefficient	Associated *P*-level	Correlation coefficient	Associated *P*-level
PD	0.66	0.03	0.57	0.06
EC	−0.25	0.46	−0.23	0.50
PT	−0.02	0.95	0.37	0.26
FS	−0.42	0.20	−0.17	0.61

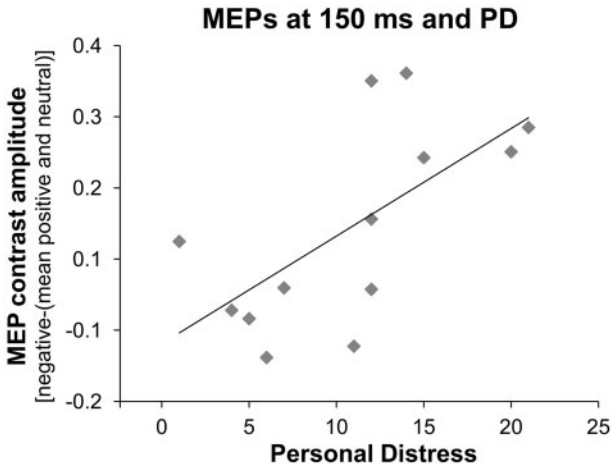

Fig. 3 Simple correlation between MEP contrasts at 150 ms (amplitude during negative pictures minus mean amplitude in the positive and neutral conditions) and Personal Distress subscale of the Interpersonal Reactivity Index.

DISCUSSION

Although it is widely assumed that emotions prime the body for action, the effect of visual perception of natural emotional scenes on the dynamics of the human motor system have rarely been investigated. In the present study we directly tested the hypothesis that perception of emotionally negative scenes triggers fast reactivity in the corticospinal system. We used single-pulse TMS to monitor changes in excitability of the dominant hand cortical motor representation while participants observed and actively categorized pictures from the IAPS database. We found that seeing negative pictures increased the amplitude of MEPs from the right FDI and APB muscles at 150 ms from stimulus onset. The magnitude of this early increase in hand motor reactivity was predicted by interindividual differences in the

disposition to experience personal distress. Moreover, the early motor excitability increase was followed by a comparable motor facilitation for both positive and negative pictures detected at 300 ms. These findings suggest that perception of natural emotional scenes dynamically modulates the functional state of the human corticospinal system, with faster reactivity for potentially threatening scenarios. Moreover, they highlight a functional link between interpersonal anxiety-related personality traits and motor reactivity to complex negative emotional scenes.

The neural network involved in the perception of emotional scenes has been highlighted in a series of functional imaging studies (see Sabatinelli *et al.*, 2011, for a recent meta-analysis of 57 studies). This network includes not only occipitotemporal visual regions but also medial frontal cortices (orbitofrontal and cingulate cortex) that are densely connected to the motor cortex either directly or via premotor and supplementary motor areas (Morecraft and Van Hoesen, 1998; Cavada *et al.*, 2000; Oliveri *et al.*, 2003) and may thus provide a cortical pathway for emotional cues to modulate motor excitability (Pessoa and Adolphs, 2010). Remarkably, motor reactions to aversive visual stimuli may also be implemented through predominantly subcortical routes as suggested by studies on brain damaged patients with permanent cortical blindness (Tamietto *et al.*, 2009). Moreover, imaging evidence indicates that subcortical structures (i.e. pulvinar, thalamus and amygdala) are active during perception of complex emotional scenes (Sabatinelli *et al.*, 2011) and, in principle, these structures may provide additional signals to different segments of the motor pathway during processing of emotional stimuli (Tamietto and De Gelder, 2010; De Gelder *et al.*, 2011).

ERP studies have highlighted the cortical dynamics of emotional scene processing and, particularly relevant to the present findings, they have reported an initial greater reactivity for negative scenes in occipitotemporal regions (within 100–200 ms from stimulus onset; Olofsson *et al.*, 2008) and, in some cases, also in frontal regions. For example, Carretié and colleagues (2001, 2006) reported that seeing negative scenes increases the amplitude of frontal positive ERP components with latencies in the 160–200 ms range which are thought to reflect the activation of medial prefrontal cortices (see also Kawasaki *et al.*, 2001; Northoff *et al.*, 2000). Our data significantly expand these findings by demonstrating that this early 'negative bias' is not limited to neural regions involved in sensory processing and affective evaluation but extends to the cortical motor representation of the dominant hand, supporting the notion that emotional cues drive action preparation in the brain and that potential threats require particularly quick motor reactions to secure the survival of the organism (Lang *et al.*, 2000; Öhman and Mineka, 2001; Frijda *et al.*, 2009; Carretié *et al.*, 2009).

The early motor facilitation for negative pictures appears strictly related to interindividual differences in personal distress but not empathy dispositions. Personal distress is an aversive, self-focused emotional reaction to the negative state of another, and the PD subscale of the IRI assesses this anxiety-related interpersonal disposition (Davis, 1996). While personal distress may counteract mature forms of empathy (Batson *et al.*, 1997; Lamm *et al.*, 2007; Avenanti *et al.*, 2009a), studies have reported that participants who score high on the PD scale show enhanced reactivity of the insula when seeing negative facial expressions (i.e. pain or disgust, Saarela *et al.*, 2007; Jabbi *et al.*, 2007). Seeing stimuli depicting painful stimulation of the body of another reduces motor excitability, an effect that may be due to the 'resonant' activation of pain representations in the observer (Minio-Paluello *et al.*, 2006; Avenanti *et al.*, 2009b). Interestingly, participants with high PD scores tend to show increased motor excitability when seeing the pain of others (Avenanti *et al.*, 2009a), in line with the notion that anxiety-related traits are associated with greater motor excitability (Wasserman *et al.*, 2001). Notably, greater PD scores are also associated with heightened action readiness but weaker motor control when facing negative images, suggesting that increased motor reactivity may be nonfunctional (Ferri *et al.*, 2010). Our study is consistent with such evidence and supports the view that anxiety-related traits influence the way in which social and emotional signals are processed in the brain (Moriguchi *et al.*, 2006; Lawrence *et al.*, 2006; Kret *et al.*, 2011; Azevedo *et al.*, 2012).

The early motor facilitation for negative pictures may seem at odds with previous TMS studies testing the excitability of the left motor cortex during perception of emotional scenes. Most of these studies reported comparable motor facilitation of right hand muscles for positive and negative pictures, either during passive observation (Hajcak *et al.*, 2007) or active categorization of the images (Borgomaneri *et al.*, 2012), or when planning a movement during observation of task-irrelevant pictures (Coombes *et al.*, 2009). Similar findings were also reported by Baumgartner and colleagues (2007) during passive presentation of emotional scenes and emotionally congruent auditory stimuli. Notably, in all such studies MEPs were collected at 300 ms from picture onset (Borgomaneri *et al.*, 2012) or at a later time (Hajcak *et al.*, 2007; Baumgartner *et al.*, 2007; Coombes *et al.*, 2009), and ERP studies suggest that electrophysiological responses to positive and negative pictures are similar in the 300–600 ms range (Olofsson *et al.*, 2008). Thus, our study confirms these temporal dynamics and, on the other hand, indicates the presence of an earlier modulation of the motor cortex when facing emotionally negative scenes.

While MEPs were collected at two discrete time points, it is likely that during perception of emotional scenes the excitability of the observer's motor cortex gradually changes over time, in line with traditional models of continuous information processing (Miller *et al.*, 1992; Massaro and Cohen, 1995). Future studies testing motor excitability at earlier time windows and with more intervals have the potential to disclose how neural responses to emotional scenes gradually build up (see Michelet *et al.*, 2010; Barchiesi and Cattaneo, 2013 for recent examples in the domain of action execution and observation).

It is worth noting that the reported modulations of motor excitability occurred in the left hemisphere. Traditionally, two theories have linked emotion perception to the issue of hemispheric laterality. According to one view, the right hemisphere is specialized to process all emotions, whereas another view suggests that the right and the left hemispheres are relatively specialized in processing negative and positive emotions, respectively (Silberman and Weingartner, 1986; Davidson and Hugdahl, 1995; Borod *et al.*, 2000). Since our results showed that negative scenes are able to modulate the left motor cortex, none of these laterality effects can be considered as confounds for the reported changes in motor excitability. Further studies are needed to directly investigate how perception of negative and positive emotional scenes may differentially influence neural motor dynamics in the two hemispheres.

That negative scenes could be particularly adept at facilitating action mechanisms was already suggested by behavioral studies exploring motor performance and action readiness (Coombes *et al.*, 2005, 2009; Naugle *et al.*, 2010). This notion has also been supported by studies reporting enhanced motor cortex plastic reactivity to repetitive TMS during presentation of negative pictures (Koganemaru *et al.*, 2012), as well as increased behavioral imitation (Grecucci *et al.*, 2011) and motor and premotor cortex response to the observation of others' actions (Enticott *et al.*, 2012; Ferri *et al.*, 2013) when action stimuli were primed by unpleasant cues. Moreover, increased EEG motor readiness potentials were found when planning to grasp unpleasant relative to pleasant or neutral objects (de Oliveira *et al.*, 2012) or when moving a finger after negative relative to neutral pictures (Grecucci *et al.*, 2009). Relevant to the present findings are TMS studies in which MEPs were recorded during action execution. In a

first study participants pressed a button when seeing emotionally negative IAPS pictures (Oliveri *et al.*, 2003). In such a condition hand motor excitability was greater than in neutral control conditions. However, only negative and neutral conditions were tested and thus it was not clear whether motor facilitation was driven by unpleasant valence or emotional arousal. More recently, Van Loon *et al.* (2010) asked participants to respond to symbolic targets during presentation of task-irrelevant IAPS pictures. MEPs were recorded at various delays from target onset. Overall, MEP amplitude was larger during positive and negative than during neutral pictures, similarly to previous studies in which MEPs were recorded at rest (Hajcak *et al.*, 2007; Baumgartner *et al.*, 2007; Coombes *et al.*, 2009; Borgomaneri *et al.*, 2012). However, when the TMS pulse was delivered during actual finger movement, MEPs were larger for negative relative to positive and neutral pictures.

In sum, despite the long-held view that negative stimuli require fast processing and reactions, to date, previous TMS studies on the perception of natural emotional scenes tested the excitability of the left motor cortex only in a relatively late temporal window. In these conditions a negative bias was detected only when the motor system was preactivated (Van Loon *et al.*, 2010). Our study provides direct evidence that a negative bias can be detected also at rest when motor excitability is tested early. This negative bias is then followed by a comparable increase in motor excitability for both negative and positive stimuli. In conclusion, our study highlights the temporal dynamics of the human corticospinal system during perception of natural emotional scenes.

SUPPLEMENTARY DATA

Supplementary data are available at *SCAN* online.

CONFLICT ON INTEREST

None declared.

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